Increasing variation in population size and species composition ratio in mixed-species heron colonies in Japan

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Long-term population dynamics of colonial herons and egrets are well documented in Europe and the USA, but not in East and South-East Asia. Here the population dynamics of mixed-species colonies from 2002 to 2011 in Ibaraki prefecture, east Kanto, Japan, are reported. From censuses based on a combination of aerial and ground surveys, the number of breeding colonies was found to vary from 15 to 20. The population dynamics of Great Egret *Casmerodius albus* and Black-crowned Night Heron *Nycticorax nycticorax* remained relatively constant, while Grey Heron *Ardea cinerea* and Intermediate Egret *Mesophoyx intermedia* increased, but Little Egret *Egretta garzetta* and Cattle Egret *Bubulcus ibis* decreased. When data for the six species were combined, the sum of their populations was almost constant, but variation increased in colony size, species composition ratio and the number of years that individual colonies existed. The population of colonies typically ranged from 200 to 2,000 individuals up to 2004, but smaller (under 200 individuals) and larger (over 2,000 individuals) colonies appeared after 2006. Increased variation in the number of consecutive years colonies existed was closely related to increased variation in colony size. Increased variation in species composition ratios in colonies was not a by-product of the increased variation in colony size, and the occurrence of colonies dominated by Grey Heron, Intermediate Egret or Black-crowned Night Heron after 2006 played an important role in the structural changes of mixed-species colonies.

INTRODUCTION

Herons and egrets (Ardeidae) are commonly found in aquatic habitats worldwide (Kushlan & Hafner 2000). In Europe, long-term population trends of such species have been well investigated, and some factors that explain how and why population sizes fluctuate at regional level have been revealed: cold winters (Stafford 1971, Reynolds 1979, Hafner & Fasola 1997, Fasola *et al.* 2010), rainfall (McKilligan 2001), water level (Grüll & Ranner 1998), habitat conditions (Tourenq *et al.* 2000, 2004), aquaculture (Fleury & Sherry 1995) and human disturbance (Fasola *et al.* 2010). In East and South-East Asia, long-term records of breeding populations of colonial nesting herons and egrets only exist in Hong Kong and Vietnam (Kushlan & Hafner 2000, Wong & Young 2006). Lack of local information makes it difficult to assess the current status of these birds.

In Japan Grey Heron *Ardea cinerea*, Great Egret *Casmerodius albus*, Intermediate Egret *Mesophoyx intermedia*, Little Egret *Egretta garzetta*, Cattle Egret *Bubulcus ibis* and Black-crowned Night Heron *Nycticorax nycticorax* breed in mixed-species colonies. Nationwide research was carried out in 1980 and 1992 (Research Division of the Wild Bird Society of Japan 1981, Environmental Agency of Japan 1994), and it was reported that single- and mixed-species colonies were distributed throughout Japan's lowlands. Although there are many observations of colonies in various areas, long-term local population trends have only been reported by Narusue (1992) and Matsunaga *et al.* (2000).

Narusue (1992) argued that both the populations and the average colony size of these species declined from the 1940s to 1992 in Saitama prefecture, west Kanto Plain, due to loss of foraging areas and use of agricultural chemicals. Changes in the irrigation of rice fields from shallow earth ditches to deep concrete-walled channels and the decline in aquatic prey caused the decline of Intermediate Egret (Narusue & Uchida 1993, Lane & Fujioka 1998), the commonest egret until the 1960s, but now categorised as 'near threatened' (Ministry of the Environment 2002). In contrast, a long-term study of Grey Herons in Hokkaido by Matsunga *et al* (2000) reported an increase in population and the number of colonies. There are currently no other reliable data to assess population trends of herons and egrets in Japan.

The Environmental Agency of Japan (1994) showed that in Ibaraki prefecture, east Kanto, Japan, both the average colony size and the population of Intermediate Egret were large compared to elsewhere in Japan, and this suggested that data from this area could provide important information for future assessment of populations of colonial breeding herons and egrets in Japan and other parts of Asia. In this study, colony censuses were carried out from 2002 to 2011 in Ibaraki prefecture to investigate trends in these populations using a combination of aerial and ground surveys. The changes are discussed here with reference to the trends in population dynamics of each species, changes in the nesting vegetation and the number of consecutive years that colonies existed.

METHODS

Study area

The study focused on Ibaraki prefecture and parts of Tochigi and Chiba prefectures in Honshu, central Japan (35.783°–36.767°N 139.767°–140.683°E) (Figure 1). The area is in the east Kanto Plain, near Lake Kasumigaura, and includes six major rivers: Kuji, Naka, Sakura, Kokai, Kinu and Tone. The north is mountainous, but the predominant land use in other areas is farming, with large areas along the rivers being used for rice production. There are also lotus fields near Lake Kasumigaura, areas of lowland forest and human habitations. Japan started a national project to consolidate rice production in 1963; this included extending irrigation ditches, improving service roads, and enlarging fields to facilitate mechanised farming equipment. It was largely complete by 1980 (Himiyama & Kikuchi 2007), but continued in part of the study area into the last decade, being 78% complete by 2010 in Ibaraki prefecture. The climate of the region is moderate with an annual average air temperature of 14.0 ± 0.1°C and an annual precipitation of 1,388.2 ± 54.3 mm. Despite a small annual decrease in rice cultivation, neither climate nor land use showed obvious changes during the study period (Figure 2).

The herons and egrets breed from March to August, but there is considerable variation from species to species (Figure 3). The Grey Heron arrives first in March, Great Egret, Little Egret, and Black-crowned Night Heron arrive in April; these species are residents and wanderers, and some individuals winter in this area. Finally, the migrant species arrive, Intermediate Egret in late April and Cattle Egret by early May (A. Abe *in litt.* 2006). Usually Grey

Figure 1. Locations of colonies from 2002 to 2011. Grey regions show an altitude greater than 100 m where the distribution of egrets is lower. Dots enclosed by a circle are considered to be historically identical colonies. Exceptionally, there are two cases in which the nearest-neighbour distance is shorter than 6.47 km; (1) $\mathbf{I}_{20} - \mathbf{L}_{30}$: because **L** was newly established in 2010 and consisted of Grey Herons *Ardea cinerea* and Great Cormorants *Phalacrocorax carbo*, we assumed **L** was different from **I**. (2) $\mathbf{Q}_{40} - \mathbf{R}_{41,42}$: **Q** was newly established in 2006, whereas Koshida (2007) reported that **R** has existed since 1984. It is difficult to accept that **Q** and **R** are one colony.

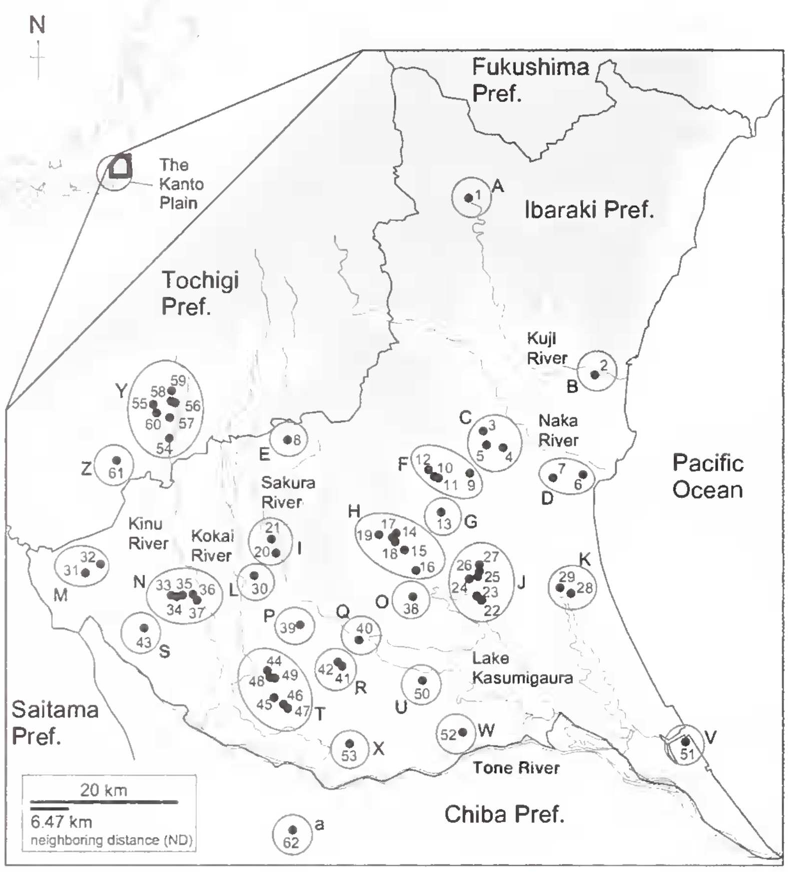
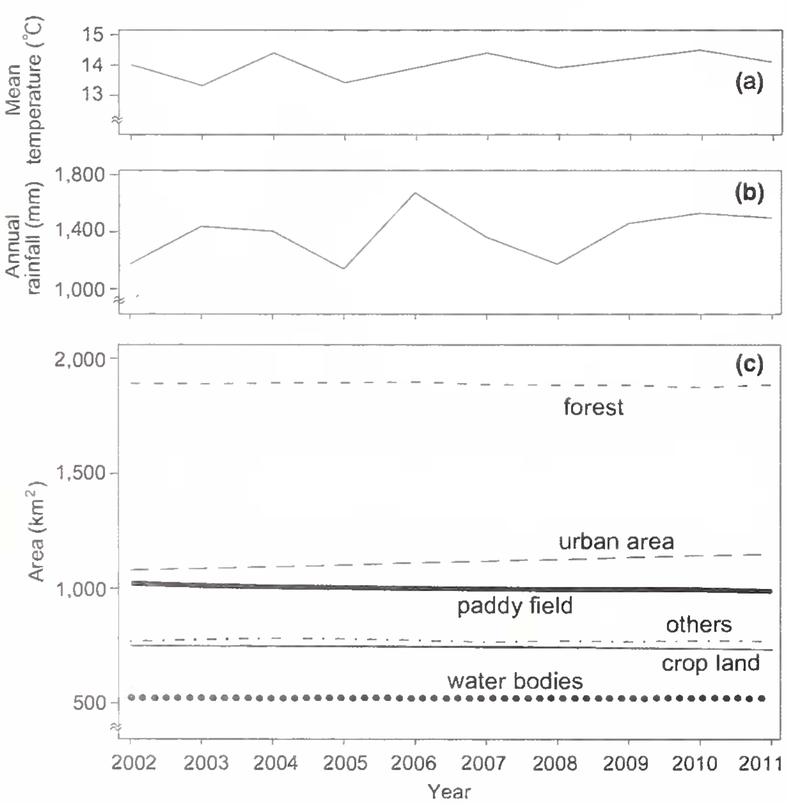


Figure 2. Changes in **a.** mean temperature, **b.** annual rainfall, and **c.** areas of six land-use types from 2002 to 2011 in Ibaraki prefecture, which was the main region of the study area (6,096 km²). 'Paddy field' includes both rice paddies and lotus fields, and 'others' includes parks, golf courses, and uncultivated fields. Data were downloaded 8 June 2013 from http: //www.data.jma.go.jp/obd/ stats/etrn/index.php for climate and http: //www.pref.ibaraki.jp/bukyoku/kikaku/mizuto/ ibarakinotochi/25/ibarakinotochi.htm for land use.



Heron and Black-crowned Night Heron are nocturnal, but during the breeding season they are also active during the day.

Colonies were located in bamboo thickets, trees or a mixture of both. Bamboo thickets were composed of Moso Bamboo *Phyllostachys pubescens*, Simon Bamboo *Pleioblastus simonii* or Dwarf Bamboo *P. chino*. Coniferous tree sites consisted mainly of Japanese Red Pine *Pinus densiflora*, Japanese Cedar *Cryptomeria japonica* and Japanese Cypress *Chamaecyparis obtusa*; broadleaf tree sites were mainly Japanese Zelkova *Zelkova serrata*, Japanese Oak *Quercus serrata* and Yoshino Cherry *Prunus × yedoensis*.

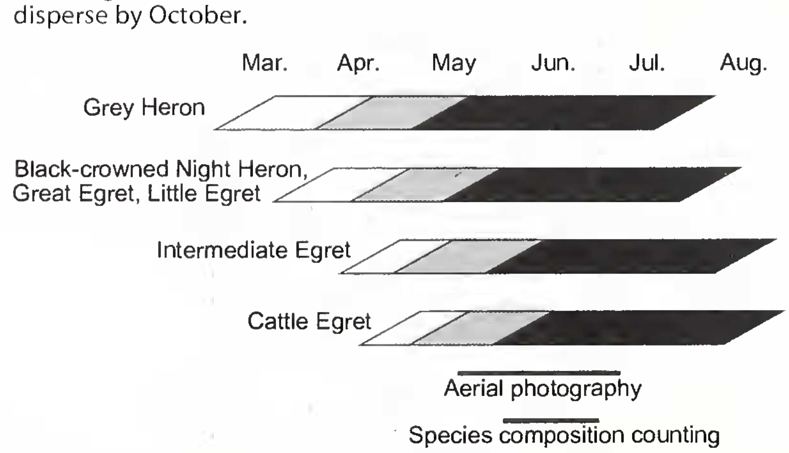
Census of colonies

Colonies have been recorded in the area over the last 25 years (Koshida 2007) and have high site fidelity (Custer *et al.* 1980, Frederick *et al.* 1996); between March and early May, 93 ± 0.02% of the colony sites were found by checking the places where colonies had been located in previous years. When a colony was abandoned, checks were made to determine whether other colonies had formed nearby. Local literature and personal communication were used to locate colonies that had not been found during the authors' own field work. Site vegetation was recorded by identifying bamboo or tree species holding at least one nest.

In small colonies of fewer than about 50 nests, if all the nests were visible from outside or within the site, the nests of each species were counted directly from the ground, and the breeding population estimated by doubling the number of nests counted. In most cases, ground-based counts were impossible due to colony size, the impenetrable nature of dense bamboo thickets, or other vegetation, such as tall trees, that made nests invisible. Hence, counts were made using a combination of aerial and ground surveys, following the method of Fujioka *et al.* (2001).

For aerial surveys, a small 'Sky Surfer' radio-controlled paraglider was used (Green Corporation, Japan, Plate 1a). This equipment is quieter than fixed-wing aircraft or helicopters commonly used for bird colony censuses (Kushlan 1979, Rodgers *et al.* 2005), and very suitable in this case where more than 80% of the colonies were close to residential areas. Aerial photographs of each colony were taken at an altitude of 30–50 m just before sunrise (about 04h00) when most birds were in the colony. Photography was started in mid-May after arrival of Cattle Egrets, and was continued until early July when distinguishing between growing nestlings and adults became difficult (Figure 3). Aerial photographs were taken once during that period at each site. All individuals of the four light-coloured species (Great Egret, Intermediate Egret, Little Egret, and Cattle Egret) in the images were counted (Plate 1b). For large colonies, several photographs were used to obtain a complete composite image of the colony.

Figure 3. Breeding period of each species in the study area showing the timetable of aerial surveying and species composition counts. White, grey, and black shading show arrival and nest building, incubation, and chick-rearing periods, respectively. The parallelogram shapes indicate the variation in individual breeding periods. After breeding is over, some birds continue to roost in the colonies but all disperse by October.



GREEN CORPORATION

M. MASHIKO

Plate 1.
a. Sky Surfer in flight.
b. An example of aerial photographs that show one part of a composite photograph.

Because it was not feasible to identify the light-coloured species only from the photographs, and because the two dark-coloured species (Grey Heron and Black-crowned Night Heron) were difficult to count in the photographs, species composition ratios—the proportion of each species within a colony—were estimated using data from ground surveys. The number of individuals of all species going in and out of each colony for a period of 30 minutes in the daytime were counted using binoculars. It was very difficult to identify to species level white egrets flying in and out at the same time, so the viewing range of each observer was restricted by setting a common range of observation, approximately a 30° field of vision. In the case of large colonies, surveys were carried out from two or three different directions. Ground surveys were made once or twice in June, the peak chick-rearing period (Figure 3), when all species engage in frequent foraging flights. Thirty minutes is much shorter than the typical duration of one foraging flight and it was assumed that each individual counted, whether arriving or departing, was observed only once during the observation period and therefore the observed proportion of each species reflects the species composition ratio of the colony.

The total estimated number of individuals in the colony (T = colony size) was calculated using $T = \frac{A}{1-x}$, where A is the actual number of light-coloured individuals counted from aerial photographs, and x is the sum of the proportion of Grey Herons and Black-crowned Night Herons obtained from the ground survey. The estimated population size of each species in the colony was obtained by multiplying the colony size by the proportion of each species.

Data analyses

To determine the number of colonies each year, the number of observed colony sites was first counted. But the number of sites itself was not taken to be the number of colonies because a few colony sites were very close to each other despite foraging ranges having radii of about 10 km, and sometimes over 20 km (Nabeya 2011). An earlier study showed that heron colonies are evenly distributed to avoid overlap of foraging sites (Gibbs *et al.* 1987). Consequently if colony sites were located close together, they were grouped together and counted as a single colony because their foraging areas overlapped substantially. To determine which sites should be counted as a single colony, the half of the mean nearest-neighbour distance (ND) of observed colony sites for each year was used. If more than one colony site was located within the ND, colony censuses were carried out at each site, the data were combined and it was counted as a single colony.

Colonial birds have been found to have high site fidelity (Custer *et al.* 1980, Frederick *et al.* 1996); every year some colonies returned to the same locations as the previous year, some birds were abandoned and new ones were established. To obtain the number of consecutive years (NCY) each colony existed, the number of years from first establishment at the location was counted. The movement of a colony was also considered and when abandonment and new establishment occurred in neighbouring locations in successive years, the new site was assumed to be a descendant of the abandoned one, e.g. abandonment was sometimes caused by vegetation loss through natural causes or felling and the colony was often re-established nearby. The ND was used to determine a reasonable displacement distance of a colony and it was assumed that each colony had a domain of attraction of half the average distance between the next nearest sites. Thus, colonies consecutively established at the same site or at a different site within a radius of the ND were counted as a single colony. Koshida (2007) was used as data source of the NCY of colonies established before 2002; consequently the NCY ranged from 1 to 36 years rather than being limited to the period of this study.

The population of each species was calculated annually using the mean population size per colony rather than summing the population sizes for all colonies with census data. This approach was used because aerial and ground surveys produced only partial data due to practical difficulties—problems in taking aerial photographs and/or delays in detecting colony sites. The simple sum of colony population sizes would have been inappropriate because it is an increasing function of the number of colonies with census data. The percentage of colonies surveyed increased from 78% in 2002–2004 to 94% in 2006–2011. (Data from 2005 were excluded because aerial and ground surveys were limited to only 5 out of 18 colonies.) Thus, the overall total population of the target species reflect the mean colony sizes rather than the total number of individual birds in the study area.

To evaluate difference in colony size, species composition ratio, and NCY among colonies, the coefficient of variance (CV) for each year was calculated. For species composition ratio, the proportional similarity index (Whittaker 1952) was calculated for each colony every year as $\frac{\Sigma|p_i - \overline{p_i}|}{2}$, where p_i is the proportion of species i in one colony and $\overline{p_i}$ is the mean proportion of that species in all colonies surveyed in that year. The index ranges between zero and unity: zero means completely different and unity means completely equal. Then the CV of proportional similarity of the species composition ratio was obtained for each year.

Ten years is too short for ordinal time series analyses, so randomisation tests were done to assess temporal trends in the number of colonies, population sizes of each species, sum of the population sizes of the six species, colony sizes and CVs of three variables (colony size, species composition ratio and NCY). In a randomisation test, the linear regression coefficient (β) of a target variable based on the original data was obtained first. Next the data were shuffled 30,000 times and compared beta with the linear regression coefficients (β's) of the shuffled data to obtain one-sided P-values to assess whether the target variable was increasing or decreasing. Sensitivity analyses of the population of each species against the three CVs (colony size, species composition ratio and NCY) were performed. Generalised linear models specifying population sizes of the species as explanatory variables and CVs as dependent variables were constructed, using Gaussian distribution with an identity link function for all model fitting. The most suitable models based on Akaike's information criterion values were chosen and the coefficients of explanatory variables of the models as sensitivity against dependent variables were considered.

If the CVs of colony size and species composition ratio show parallel changes, there is a possibility that the variation in species composition ratios increased as a by-product of the increase of variation in colony sizes. To examine this possibility, a randomisation test was performed to determine whether the variation in species composition ratios was solely caused by a sampling bias according to the variation in colony size. First a hypothetical total number of herons that consisted of the six species was prepared. The species composition ratio of the whole number of herons was arbitrary. Next multiple colonies with equal colony sizes from the total number of herons were sampled. Then proportional similarities of species composition ratios of these hypothetical colonies against the species composition ratio of the whole number of herons were calculated. Proportional similarities for hypothetical colonies of the same number but with different colony sizes were also calculated. Finally, the variance of the proportional similarities between equal and unequal size colonies were compared, and the probability that proportional similarities of unequal size colonies were larger than or equal to those of equal size colonies with 10,000 iterations was obtained.

To evaluate changes in nesting vegetation, the Friedman test was used to analyse whether the vegetation of colony sites changed from year to year. Nesting vegetation consisted of one or a mixture of the following three types: bamboo thickets, coniferous trees and broadleaf trees; there were seven types in total.

Finally, a randomisation test was performed to determine whether there was a positive correlation between NCY and colony size among colonies by reshuffling the year record so as to randomise the consecutive colony-size dynamics of each colony.

All statistical analyses were conducted using R ver. 2.13.0 (R Development Core Team 2011). Data are presented as mean ± SE throughout. The randomisation test on the relationship between the variation of population sizes and that of species proportion ratios was also conducted with R. All R scripts for the above statistical analyses are available from the authors.

RESULTS

During the 10-year period, there was an average of 19 colony sites in the study area every year (19.10 ± 0.72 colony sites, n = 10); cumulatively 191 colony sites were used over the 10 years. Some colonies were in the same locations for more than one year, and a total of 62 colony sites were used (1 to 62 in Figure 1). Colony sites were separated by an average of 13 km (mean ND over 10 years 12.95 ± 8.39 km, n = 191), so the ND was defined as within 6.47 km. Hence, these 62 colony sites were categorised into 27 colonies (**A** to **a** in Figure 1) because colony sites consecutively established at different locations within a 6.47 km radius were considered a single colony. Six of 27 colonies were made up of two or three colony sites in at least one breeding season, and the median distance between them was 1.44 km (range: 0.32–5.12 km, 10 combinations of colony sites in all). Finally, the annual number of colonies increased gradually (β = 0.382, P = 0.006) from 15 to 20 (Figure 4a).

In the case of Intermediate Egret and Black-crowned Night Heron, the average population per colony was relatively large (about 300 individuals) and these species remained dominant throughout the 10-year period (Figure 4b). Conversely, it was small (about 50 individuals) for Great Egret and Grey Heron, and intermediate (about 100 individuals) for Cattle Egret and Little Egret. The sum of the population of the six species (mean colony size) ranged from 726 to 966 individuals and remained almost constant (β = −4.301, P = 0.342).

The population trends of each species varied (Figure 4b). Grey Heron and Intermediate Egret increased (Grey Heron: β = 9.575, P < 0.001; Intermediate Egret: β = 9.519, P = 0.033), whilst Little Egret and Cattle Egret decreased steadily (Little Egret: β = −2.069, P = 0.002; Cattle Egret: β = −20.672, P < 0.001). The Black-crowned Night Heron population fluctuated over the years but remained almost constant (β = 9.311, P = 0.145). The Great Egret population was small but almost constant (β = 0.036, P = 0.492).

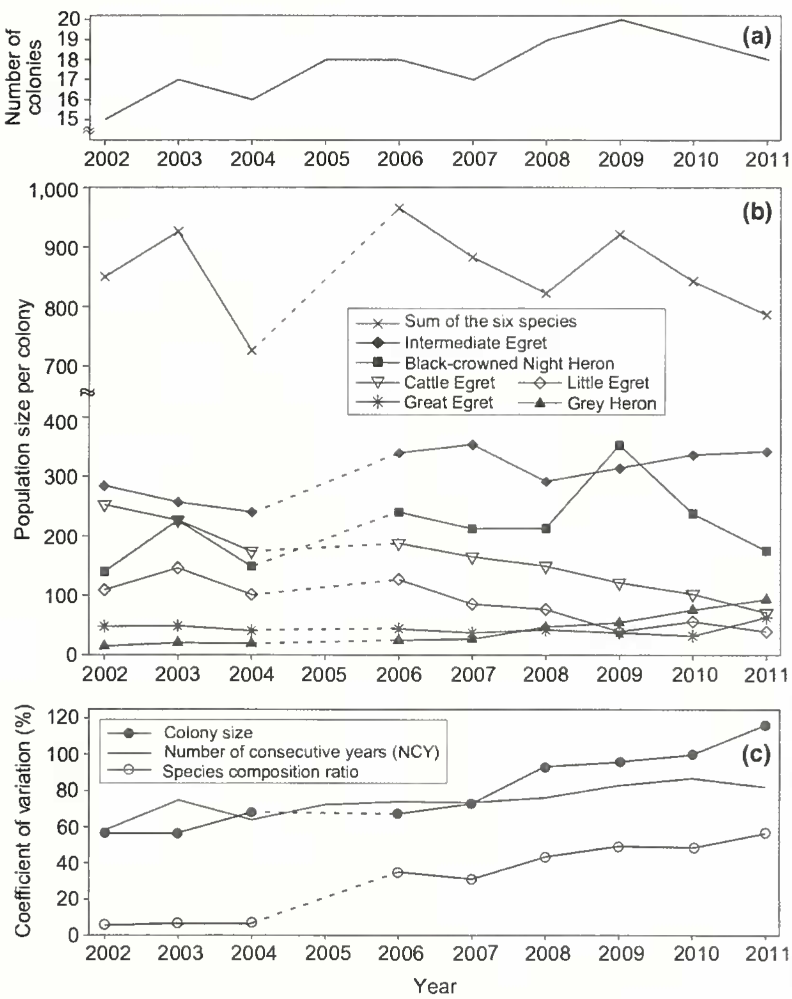
Colonies were very variable in size, and the CV of colony size continuously increased (Figure 4c) over the ten years (β = 7.510, P < 0.001). Colonies ranged from 200 to 2,000 individuals until 2004, while smaller (under 200 with minimum 8 individuals) and larger (over 2,000 with maximum 3,280 individuals) colonies appeared after 2006. Between 2008 and 2011, the smaller and larger colonies increased from 33% to 41% of colonies surveyed.

In parallel with the increase in the CV of colony size, the CV of proportional similarity of species composition ratios increased (Figure 4c), especially after 2006 (β = 7.002, P < 0.001). Until 2004, most colonies consisted of five species (Great Egret, Intermediate Egret, Little Egret, Cattle Egret and Black-crowned Night Heron), and the composition ratio was similar among surveyed colonies (mean proportional similarity = 0.86 ± 0.02, n = 43). Grey Heron bred in only three, six and seven colonies in 2002, 2003 and 2004, respectively. Until 2004, the composition ratios of the Intermediate Egret and the Cattle Egret were higher than those of other species in half of the surveyed colonies in accordance with their large population (Figure 4b), but no species became dominant (over 50% of the composition ratio). After 2006, 37% of all surveyed colonies were dominated by the Grey Heron, Intermediate Egret or Black-crowned Night Heron, and differences in the species composition ratios among colonies increased.

The CV of the NCY also increased gradually (Figure 4c) (β = 2.453, P < 0.001). Eight colonies persisted between 2002 and 2011; the remainder were abandoned or newly established. Every year 1–4 colonies were abandoned and 0–3 were established. Considering the period prior to this study, 14 out of 27 colonies had existed before 2002 and 4 had persisted for over 25 years.

Table 1 shows the results of the sensitivity analyses of population of each target species against three CVs. Increase in the

Figure 4.
a. Changes in the number of colonies between 2002 and 2011.
b. Changes in population of each species per colony of and the sum of the six species.
c. Changes in the coefficient of variation (CV) of colony sizes, number of consecutive years (NCY), and species composition ratios. For the changes in population size and CVs of colony sizes and species composition ratios, the year 2005 is not shown because aerial and ground surveys were limited to only 5 out of 18 colonies.



CV of colony sizes was explained by the increasing Grey Heron population, and the increase in the CV of species composition ratios was also explained by the increasing Grey Heron population, and marginally explained by the increasing Intermediate Egret population. The increase in the CV of NCY was explained by the increasing Grey Heron population and the fluctuating, though statistically constant overall, population trend of the Black-crowned Night Heron.

The randomisation test to determine whether the variation in species composition ratios increased as a by-product of the increase in variation of colony sizes did not reveal a significant result: the probability that the proportional similarities between unequal size colonies would be larger than or equal to those of equal size colonies was almost even (0.538). The increase of variation in species composition ratios could not solely be caused by the increase of variation in colony sizes.

Changes in vegetation of the colonies were significant over the years ($\chi^2 = 25.2$, df = 6, $P < 0.001$) (Figure 5). While the vegetation in most colonies included bamboo until 2004, after 2008 more than half the colonies were located in trees.

The slope obtained by a linear regression analysis of colony sizes against NCY (43.05 ± 5.43) was significantly larger ($P < 0.001$) than slopes obtained by the randomisation test where the year record was shuffled for each colony so as to randomise consecutive colony-size dynamics (Figure 6). This randomisation test indicates that there was a positive correlation between colony sizes and the NCY for the colonies.

Table 1. Sensitivity of population sizes against CVs. βs are coefficients of the best fit generalised linear model with Gaussian distribution and identity link function. R^2 = (null deviance - residual deviance)/(null deviance). CS: colony size, SCR: species composition ratio, NCY: number of consecutive years.

	CV of CS		CV of SCR		CV of NCY	
	β	P	β	P	β	P
Grey Heron	0.351	0.054	0.449	0.009	0.307	0.016
Great Egret						
Intermediate Egret			0.168	0.077	0.047	0.193
Little Egret	−0.133	0.169			0.124	0.101
Cattle Egret	−0.119	0.179				
Black-crowned Night Heron			0.081	0.116	0.072	0.020
Akaike's information criterion	56.329		65.833		59.157	
R^2	0.975		0.920		0.902	

Figure 5. Changes in colony vegetation. See description of study area for details of species.

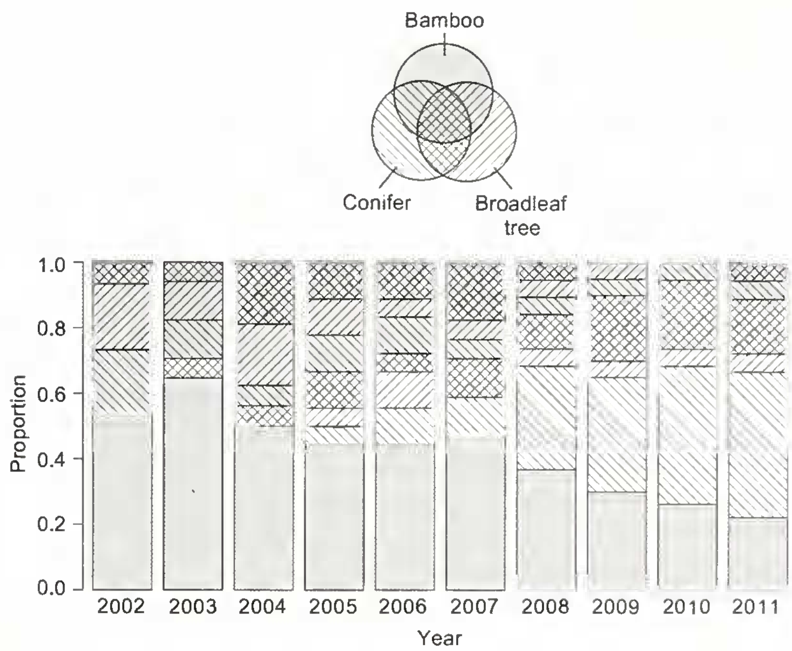
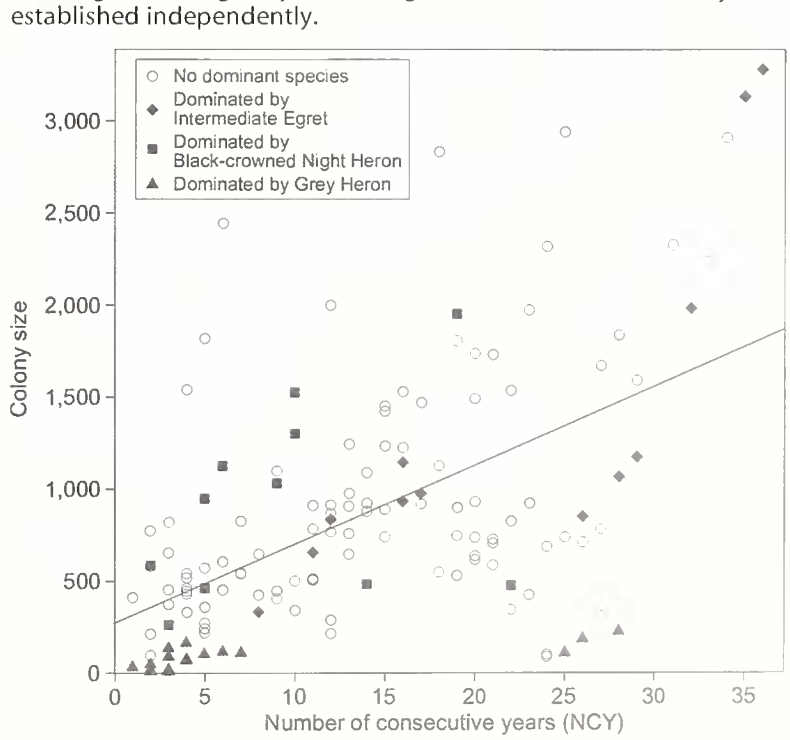


Figure 6. Relationship between colony size and longevity. Each dot represents a colony censused in a particular year (n = 141). The regression line was obtained by a linear regression analysis of colony sizes against longevity assuming that each annual colony was established independently.



DISCUSSION

The survey in Ibaraki prefecture from 2002 to 2011 indicated that the number of breeding colonies (average 19) increased slightly and mean colony size was almost constant. These results accord well with the report by the Environmental Agency of Japan (1994): there were 20 colonies in 1992 in Ibaraki prefecture, ranging in size from 15 to 2,990 individuals (CV = 112.5), and the population of these species has been relatively constant in the area for at least two decades to 2011. However, variations in size, species composition ratio and NCY among colonies increased significantly. Colony vegetation changed from predominantly bamboo thickets to tall trees. Trends in population dynamics differed: Grey Heron and Intermediate Egret increased, Little Egret and Cattle Egret decreased; and Great Egrets and Black-crowned Night Herons were relatively constant—the population of both the latter species were similar to previous reports (Research Division of the Wild Bird Society of Japan 1981, Environmental Agency of Japan 1994) and unchanged for three decades. Overall, there was no significant change in population of these colonial species in the study area during the decade, but variation in the structure of colonies and population dynamics clearly increased.

In contrast to Great Egret and Black-crowned Night Heron, the population of the other four species changed during the period (Figure 4b). Grey Heron showed the greatest population growth, which is in line with earlier reports that its population is growing in other parts of Japan (Narusue 1992, Environmental Agency of Japan 1994, Matsunaga *et al.* 2000, Sasaki 2001). In Hokkaido, Matsunaga *et al.* (2000) suggested that recent climatic warming and increase in aquaculture have provided the species with additional food resources. It is not known whether the increase of this species in other more temperate parts of Japan also depends on these factors, but its ability to respond quickly to changes in food availability (Adams & Mitchell 1995) would be expected to boost populations. The other increasing species, Intermediate Egret, was a predominant species in this area even though it has been designated as a 'near threatened' species in Japan (Ministry of the Environment 2002). Owing to the lack of current data from other parts of Japan, it is not clear whether the population has been recovering, but the abundant population in this area may be of conservation significance in Japan; monitoring of this species should continue.

Little Egret and Cattle Egret both showed a steady decline over the period; the Environmental Agency of Japan (1994) considered them to be predominant and numerous throughout Japan, including Ibaraki prefecture in 1992, and the population of both has decreased during the last two decades. Although mild winter weather contributed to their increase in France (Hafner & Fasola 1997) and rainfall drove the changes in Cattle Egret population in Australia (McKilligan 2001) and Hong Kong (Wong & Young 2006), climatic variables are unrelated to the decrease of these species in the study area because both temperature and rainfall have been almost constant (Figure 2). It seems likely that changes in food resources or foraging habitats may be contributory factors. In northern Japan, Shimada *et al.* (2005) suggested that Little Egrets might be strongly affected by the increase in population of the introduced Black Bass *Micropterus psalmoides*, which has caused a decrease of the smaller native fish species they prefer. In the absence of historical and quantitative data in Japan, monitoring studies in other regions are needed to make a complete assessment of population dynamics of these declining species.

During the study period, variations in size, species composition ratio and NCY increased (Figure 4c). Since these temporal trends showed parallel changes, there is a possibility that the variation in species composition ratios increased as a by-product of the increased variation in colony sizes; but a randomisation test contradicted this possibility, and it was concluded that the observed increased variation in proportional similarities of species composition ratio could not be solely caused by the increased variation in colony size. Another change that coincided with the study period was the change in nesting vegetation; the majority of colonies changed from bamboo thickets to trees (Figure 5). More colonies were newly established in tall trees even though bamboo thickets persisted in the area. The decrease in the number of colonies in bamboo may be due to the increase in Grey Herons because they prefer to nest near the top of tall trees. However, those results contradict the general knowledge that the target species use a wide range of nest sites, including trees, bushes, reeds and on the ground. No other species shows a particular preference for specific substrates (Kushlan & Hancock 2005). Hence, there is no strong support for the possibility that the vegetation of established colony sites affected the size or species composition ratios of colonies.

Increasing variation in NCY may help explain the increased variation in colony size and species composition ratios. These results showed that the variation in the NCY among colonies grew from year to year (Figure 4c), and there was a significant positive correlation between colony size and the NCY that a colony existed (Figure 6). Although food availability, measured as the area of potential foraging habitat around the colony, has often been thought to be the most important factor affecting colony size (Fasola & Barbieri 1978, Gibbs *et al.* 1987, Gibbs 1991, Baxter & Fairweather 1998), previous studies in this locality showed that variables related to foraging sites (areas around ponds, rivers, paddy fields and lotus fields) did not have a major impact on colony size; instead the NCY had a significant positive relationship with colony sizes (Fujioka *et al.* 2001, Tohyama 2005). Increasing variation in a colony's size is therefore closely related to the colony's longevity. As for increasing variation in species composition ratio among colonies, variations were due to the occurrence of colonies dominated by Grey Heron, Intermediate Egret, or Black-crowned Night Heron after 2006. In particular, the dominance of Grey Heron was notablet in small, recently established colonies (Figure 6). It is well known that the Grey Heron often breeds in small colonies of only 2–10 nests, while the other five species are more gregarious and usually breed in large mixed-species colonies (Kushlan & Hancock 2005). Thus, the Grey Heron population growth after 2007 might contribute significantly to the increasing variation in the species composition ratio and colony size despite its relatively small overall population (Table 1).

Overall, the local population of herons and egrets in eastern Japan seems to have remained constant for at least the last decade, in parallel with the constant climate and land use variables. Nonetheless, population dynamics of constituent species have been changing, and variations in colony sizes and species composition ratios have also increased. Such changes are revealed only by long-term and comprehensive colony census. Continuing studies are required not only to reveal the factors affecting the population dynamics of each species at a regional level, but also to establish a better understanding of relationships between each species's population and the sizes or composition ratios of mixed-species colonies.

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